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Spatial Structure and Dynamics of Salmonid Populations and Their Habitats

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SPATIAL STRUCTURE AND DYNAMICS OF SALMONID POPULATIONS AND THEIR HABITATS

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INTRODUCTION

The Rocky Mountain Research Station (RMRS) has collected considerable data on the large-scale distribution of threatened salmonids and their habitats, with a focus on bull trout (*Salvelinus confluentus*) and Chinook salmon (*Oncorhynchus tshawytscha*). The purpose of these studies is to investigate the spatial structure and dynamics of salmonid populations and their habitats. In particular, extensive data are being collected on the spatial and temporal distribution of Chinook salmon redds and potential spawning sites at watershed scales in the Middle Fork Salmon River (MFSR; Figure 1; Thurow 2000). Work conducted as part of this joint venture agreement proposes two goals: 1) evaluation of spatiotemporal patterns in the spawning distribution of Chinook salmon; and 2) determining the geomorphic controls on watershed-scale availability of Chinook salmon spawning sites. As outlined in the cooperative agreement between the University of Idaho and the RMRS, this completion report details achievements made toward these goals. Appendix A lists specific titles of presentations, posters, and peer-reviewed manuscripts that were completed in association with this work.

GOAL 1: EVALUATE SPATIOTEMPORAL PATTERNS IN THE SPAWNING ECOLOGY OF CHINOOK SALMON

Recent advances in understanding the spatiotemporal dynamics of salmonid populations have underscored the importance of metapopulation considerations for population persistence (Rieman and McIntyre 1995; Dunham and Rieman 1999). Although the exact structure of many salmonid metapopulations remains unclear, and is likely to vary by species, population status, and environment (Rieman and Dunham 2000), all of the models considered applicable to salmonids are characterized by a degree of synchrony among populations and the frequent existence of "core" areas typified by high population densities (Hanski and Gilpin 1991; Harrison and Taylor 1996). We examined patterns in redd count data to assess the prevalence of these characteristics in Chinook salmon populations within the MFSR.

Objective 1. Describe patterns in the distribution of Chinook salmon redds.

Ecological requirements of salmon are perhaps best understood in freshwater environments. Unfortunately, that knowledge is often derived from studies conducted at relatively small spatial and temporal extents (Fausch et al. 2002), which provides a poor fit to the broader spatiotemporal themes that underlie most species conservation efforts (e.g., metapopulation theory, source-sink dynamics, landscape ecology). Growing awareness of this gap, combined with advances in remote sensing, spatial sampling strategies, georeferencing capabilities, and broad usage of geographic information systems (GIS) have motivated a new generation of studies designed to understand interpopulation processes, the importance of natural disturbance regimes, terrestrial-aquatic linkages, and landscape genetics (Rieman and Dunham 2000; Costello et al. 2003; Dunham et al. 2003; Miller et al. 2003).

Here, we describe spatial and temporal patterns in network-scale redd distributions from spatially continuous, replicate surveys of georeferenced redd locations across the MFSR. Chinook salmon redds are readily observed because of their large size and high visibility for several weeks after construction. Although redd counts are often used as an index of abundance, the fact that they are the breeding structures for these fish suggests their distribution across a landscape may also serve as a useful proxy for understanding important biological and physical processes.

Results

Basinwide totals for redd counts ranged considerably—from 20 redds in 1995 to 2271 redds in 2003. Years of low escapements were intermixed with years of higher escapements, although the general trend was one of increase (Figure 2a). In addition to temporal variation, spatial variability also occurred and some segments of stream contained average redd densities as low as 0.023 redds • km^{-1}; whereas other segments averaged up to 5.2 redds • km^{-1}. Maximum redd densities for individual stream segments typically exceeded the mean density by a factor of three or four (Figure 2b).

In three subbasins, the proportion of the stream network used for spawning appeared to increase across the range of observed redd densities (Figure 3a). In two subbasins with the highest redd densities, however, the proportion of the stream network used for spawning appeared to approach an asymptote at approximately 70% of the network (Figure 3b). These asymptotes were reached at low densities (≈ 3 redds/km), and then remained constant across a three-fold density increase, which suggested that suitable reaches were rapidly colonized, but were not being fully utilized at the densities observed.

Cumulative distribution curves were used to summarize the spatial distribution of redds relative to escapement size. This technique was applied by dividing the stream network into 23 segments of equal length, calculating the proportions of redds within individual stream segments, and ranking segments within individual years. Cumulative proportions were then plotted against stream segment rank order. Comparison of curves suggests that observed spawning distributions were more clustered than random distributions (Figure 4). As redd numbers increased, distributions became less clustered, which resulted in flatter curve profiles, and decreased the proportion of redds that occurred in the densest spawning areas.

As a complement to the cumulative curve analysis, we tested whether the relative importance of individual stream segments remained constant through time using a space-time, repeated measures ANOVA. Results of the analysis suggested that a significant interaction occurred between year and stream segment ($F = 2.17, p < 0.001, df = 176$). Not unexpectedly, sample year ($F = 95.8, p < 0.001, df = 8$) and stream segment ($F = 11.5, p < 0.001, df = 22$) also had significant effects on redd abundance. Examination of variance structure through time suggested that inference from fewer than 3 – 5 years of data would have resulted in a biased view regarding the relative importance of variance components (Figure 5). With one year of data, it was impossible to estimate a year effect ($df = 0$), so all variance was attributed to segment and residual error, which inflated the apparent importance of stream segments (65 – 80% of total variation). Once multiple years of data were available, the strength of the segment effect decreased and stabilized at approximately 35% of total variation between years 3 and 5. Remaining variance components also stabilized by this time, with year, segment*year, and residual error accounting for 40%, 13%, and 12% of total variation.

Conclusions

One of the commonalities emerging from many prioritization strategies is that the best remaining areas within a species' range should be protected (Epifanio et al. 2003; Groves 2003). In this context, "best" often connotes "high density" and part of the rationale is that once limiting factors have been alleviated, protected areas can act as sources of colonists to fuel expansion into

unoccupied habitats (Schlosser and Angermeir 1995). Our work supports this idea, in that the contribution of high density areas appeared to be larger at low escapements.

A strategy focused on protection of core populations may be useful in the short-term, but longer perspectives will also be needed to accommodate the dynamics of natural systems (Hilborn et al. 2003). Even over the relatively short period encompassed by this study, we observed a significant segment*year interaction and population growth rapidly expanded spawning into areas where it had recently been absent. Over longer periods, we have documented dramatic changes in interpopulation synchronies (Objective 2) and anecdotal information suggests that spawning in mainstem areas may have once been more prevalent (Hauck 1953; Meyer and Leidecker 1999). These factors highlight temporal variation in spatial distributions, the importance of suitable, but unoccupied habitats, and the fact that populations will need room to expand as they grow (Cooper and Mangel 1998; Rieman and Dunham 2000). Conservation efforts that fail to accommodate this future growth, and which seek to protect species only in high density, or currently occupied areas, may artificially constrain populations and actually curtail future recovery possibilities. Additional details regarding this objective can be found in Isaak and Thurow (2006; Appendix A).

Objective 2. Describe patterns in spatial and temporal synchrony among Chinook redds. Aspects of metapopulation biology, including spatial diversity, temporal variation, and interpopulation processes have emerged as important considerations in conservation planning for many species (Rieman and Dunham 2000). Although it is unclear which of several metapopulation models accurately describes population dynamics in salmonid fishes, all models are characterized by some level of correlation, or synchrony, among populations through time (Harrison and Taylor 1996). Weak temporal synchrony is often regarded as beneficial because habitats vacated by local extirpations can be recolonized by dispersal from nearby populations (Sutcliffe et al. 1997), whereas strong synchrony can result in simultaneous extirpations when abundances are low (Heino et al. 1997). Discerning patterns in spatial synchrony may be equally important, as areas of covariation in demographic parameters can indicate typical dispersal distances, and therefore provide insights to ecological neighborhood size and the geographic scale at which local populations may be structured (Bowman et al. 2000).

For this objective, we explored patterns of temporal synchrony using salmon redd counts conducted by the Idaho Department of Fish & Game (IDFG) since 1955 at 13 locations within the MFSR. Temporal synchrony was examined by calculating Pearson correlations between all pairwise combinations of redd count time-series from the 13 locations. To provide a dynamic perspective, these correlations were also calculated using an 8-year sampling frame that was advanced at one year increments through each pairing of time-series.

Spatial synchrony was examined using the spatially continuous redd data described in Objective 1. Semivariograms, which measure half the average variation between data values at two points as a function of the intervening distance, were used to describe patterns in spatial variation (Rossi et al. 1992). Semivariances were calculated for a series of spatial lags, or distance classes, as:

$$\gamma(h) = 0.5\frac{1}{N(h)}\sum_{xi-xj\sim h}[z(x_i) - z(x_j)]^2 \quad (1)$$

where: $y(h)$ = semivariance at stream distance lag h, $N(h)$ = number of pairs of points (x_i, x_j), separated by stream distance h, and $z(x_i)$ = redd density in reach x_i. To apply this technique to the redd data, the stream network was partitioned into 500 m reaches and lineal redd densities were calculated for each reach. A curve was fit through the semivariance estimates for successive spatial lags, and parameters estimated from this curve were used to quantify spatial structure. The parameter we were interested in was the Range, which denotes the distance over which redd densities were autocorrelated, or spatially dependent (Figure 6).

Results

Results from the temporal synchrony analysis suggest the mean correlation among redd counts increased from an initial value of 0.2 to 0.8 as population abundance decreased (Figure 7). Coincident with stronger synchrony, the range of interseries correlations also narrowed. Early correlations ranged from negative to strongly positive, but recent correlations have all been strongly positive. These changes indicate that the likelihood of simultaneous extirpations has increased, which could have detrimental consequences for the persistence of MFSR Chinook salmon. Mechanisms accounting for changes in synchrony are not known with precision, but reductions in life history variation and decreased importance of density dependent regulation may have played roles.

Range sizes were estimated from annual redd distributions within five subbasins where most spawning occurred. Mean Range sizes varied from 3.4 – 8.8 km, with differences probably arising from variation in the distribution of spawning habitat among the subbasins (Figure 8a). Variation in Range size was positively related to differences in redd density among years (b_1 = 0.67, $p < 0.01$, $r^2 = 0.48$; Figure 8b), suggesting a density dependent effect on dispersal and the expansion of salmon populations into recently unoccupied habitats. If these Range sizes are accurate estimates of typical dispersal distances, then gene flow and population structuring may occur at geographic scales of tens of kilometers for this species.

Conclusions

Implications for management are that the resilience of Chinook salmon populations to large-scale disturbance and anthropogenic suppression may not depend solely on attempts to maintain large and productive component populations, but also on restoration of diversity that could desynchronize strongly correlated populations. Such efforts might entail promoting the existence of a broad distribution and diversity of habitats that support a wide array of life history forms and ensuring that some habitats are sufficiently spatially disjunct so that risks from catastrophic stochastic events are minimized. Protected areas should encompass more habitats than those which are currently occupied because expansion into unoccupied areas will occur as populations recover. These protected areas should be as large as possible until more is known about habitat-area requirements and possible interactions with landscape geometry, habitat productivity, and population turnover rates, all of which bear on the amount of habitat needed for species persistence. Additional details regarding this objective can be found in Isaak and Thurow (submitted; Appendix A) and Isaak et al. (2003; Appendix A).

Objective 3. Evaluate the effects of patch size, quality, and context on the distribution of Chinook salmon redds.

Declines in many fish populations have caused alarm and led to reassessments of management goals, often changing the focus from harvest-centric approaches to species persistence (Hanna 1999). As management has shifted, our perception of relevant environmental characteristics has evolved from traditional metrics that describe habitat quality to characterizations of patch geometry, or those factors related to the size and connectivity of these habitats. The new view is broader and cognizant of the fact that population persistence often depends not merely on abundance, but the exchange of individuals with nearby populations, which can either provide demographic support for flagging populations, or colonists to refound suitable habitats after local extirpations have occurred (Brown and Kodric-Brown 1977). Habitat area is important because large habitats tend to support large populations, which are less susceptible to extirpations resulting from demographic or genetic stochasticity (Lande 1993). Additionally, large habitats often contain refugia that serve as buffers against catastrophic disturbances or may support a range of life history forms that exploit the environment in different ways and provide a further buffer against extirpation (Sedell et al. 1990; Gresswell et al. 1997).

Despite the shift that has occurred regarding relevant environmental characteristics, and the implications it may have for how habitats are conserved and restored, patch geometry metrics have rarely been evaluated relative to habitat quality metrics. We used an information theoretic approach to select the best correlative models from sets of logistic regressions that linked habitat quality, size, and connectivity to the occurrence of Chinook salmon redds in spawning patches (Table 1). Field measurements that described habitat quality for 43 spawning patches in three subbasins were used in conjunction with spawning distributions determined annually from 1995 – 2004. Because of the large number of patch quality covariates, we used principal components analysis (PCA) to reduce the dimensionality of these data into a series of orthogonal axes defined by linear combinations of these variables (Vaughan and Ormerod 2005). Principle coordinate scores associated with interpretable axes that had eigenvalues greater than one were retained for use as predictors in logistic regressions.

Results

Model selection results for logistic regressions based on all years of data suggested three models were most likely (ΔAIC_c values < 2; Table 2). The sum of the Akaike weights for these models was 0.83, which indicated that 83% of the weight of evidence for patch occupancy was in these models. The best overall model was the patch geometry model, whereas the second and third best models were hybrids that contained patch geometry covariates and one or two patch quality metrics. Prediction accuracy was good, with the top models all predicting > 84% of redd occurrences at the 0.50 probability cutoff. Model quality decreased rapidly after deletion of either patch geometry covariate, and models based exclusively on patch quality metrics were the least plausible. Examination of parameter estimates for the three best models suggested that the probability of redd occurrence was strongly and positively affected by connectivity, which had a standardized effect size ≈3 times larger than patch size, the second strongest predictor (Table 3). Effects associated with patch quality metrics were small and confidence limits suggested these effects were not statistically different from zero.

Conclusions

Our results suggest that habitat geometry plays an important role in determining the distribution of Chinook salmon spawning within the MFSR. Simply knowing the size of suitable habitats and their spatial positions relative to other such habitats provides strong predictive power regarding the likelihood that a spawning patch will be used. Patch quality appeared to play a relatively minor role in determining patch occupancy, which was unexpected given numerous studies that document linkages between local habitat conditions and Chinook salmon (Roper et al. 1994; McHugh and Budy 2004) or fish populations in general (Fausch et al. 1988). Only recently, however, have fisheries scientists begun to include patch geometry in their models (Dunham and Rieman 1999; Morita and Yamamoto 2001; Koizumi and Maekawa 2004), and it remains rare for these variables to be evaluated relative to descriptors of habitat quality in model selection procedures like those employed here. If our results are generalizable, it may mean that patch geometric considerations represent basic, first-order effects that must be accounted for when attempting to understand the distribution of Chinook salmon spawning.

Our results have utility for guiding conservation and restoration activities associated with Chinook salmon. Most obviously, it appears that maintaining the size and connectivity of existing habitats should be a primary consideration in any serious conservation strategy. If resources are available for wholesale habitat restoration, the expansion of existing habitats or creation of new ones in key areas may be appropriate. Opportunities for such extensive manipulation are probably rare, as it remains likely that most activities will continue to be directed towards improving the quality of existing habitats (Bond and Lake 2003). The greatest utility this research offers, therefore, may be the strategic view that it can lend habitat restoration efforts. For example, decisions about which habitats are prioritized for treatment could be made after careful consideration of habitat size and connectivity to surrounding areas. Additional details regarding this objective can be found in Isaak et al. (submitted, Appendix A).

GOAL 2: DETERMINE GEOMORPHIC CONTROLS ON WATERSHED-SCALE AVAILABILITY OF CHINOOK SALMON SPAWNING SITES.

Here, we propose to couple fundamental hydraulic equations with digital elevation models (DEMs) to predict grain size as a function of shear stress and channel type. Spawning habitat availability will be determined by comparing predicted grain sizes to those preferred by Chinook salmon. Existing data and supplemental field studies will be used to validate model predictions of channel type, grain size, and spawning habitat availability. Future studies will expand our approach to examine the effects of sediment supply on grain size and spawning habitat availability.

Objective 1. Predict grain size and the spatial distribution of suitable spawning habitat as a function of channel hydraulics and boundary shear stress.

Grain size in gravel- and cobble-bed rivers is strongly controlled by channel hydraulics and skin friction shear stress that is imparted to the bed and responsible for sediment transport (Buffington and Montgomery 1999). In particular, the bankfull flow is the dominant discharge influencing sediment transport, substrate size, and channel morphology in many alluvial rivers (Wolman and Miller 1960; Carling 1988). The median grain size (D_{50}) that can be mobilized by the bankfull flow can be predicted from the Shields (1936) equation as

$$D_{50} = \frac{\tau}{(\rho_s - \rho)g\tau^*_c} = \frac{\rho ghS}{(\rho_s - \rho)g\tau^*_c} = \frac{\rho hS}{(\rho_s - \rho)\tau^*_c} \quad (2)$$

where τ is the total bankfull boundary shear stress defined from the depth-slope product (ρghS), ρ_s and ρ are sediment and fluid densities, g is gravitational acceleration, h is bankfull flow depth, S is channel slope, and τ^*_c is the dimensionless critical shear stress for movement of D_{50} (see review by Buffington and Montgomery 1997). The shear stress applied to the bed is influenced by channel type and associated hydraulic roughness (Buffington and Montgomery 1999). Here, we adjust τ^*_c as a function of channel type to empirically account for the effects of roughness on sediment size carried by the channel (Buffington et al. 2004). The only unknown parameters for predicting grain size in equation (2) are flow depth (h), channel slope (S), and critical Shields stress (τ^*_c), each of which will be parameterized in the below tasks. Finally, the abundance and location of suitable spawning sites can be assessed by comparing predicted reach-average grain sizes to those preferred for spawning.

Methods

Although our ultimate goal is to predict substrate size and spawning habitat availability throughout the Middle Fork Salmon stream network, initial model development was limited to areas accessible to Chinook salmon. As a result, the stream network was truncated to match the upstream extent of spawning observed during annual redd censusing efforts conducted between 1995 and 2002. These surveys were inclusive of the Middle Fork Salmon mainstem and larger tributaries in ten major subbasins and encompassed all areas known to have historically supported spawning. The truncated network comprised 638 km of stream, which was a 94% reduction from the 10,400 km blueline network depicted on 1:24,000-scale maps (Figure 9).

Within this reduced network, channel reaches were delineated between 40' contour lines on 7.5 minute topographic quadrangles, and further subdivided at tributary junctions. Reach slopes were predicted from these data and field checked with stream surveys. Slopes were surveyed in 121 stream reaches that were twenty bankfull widths long. Results demonstrate that map slopes approximate field slopes, but can differ from field values by a factor of two or more (Figure 10). These results are typical of other mountain basins (Massong and Montgomery 2000).

The same field data were used to develop local hydraulic geometry relationships for predicting reach-average bankfull depth (h) as a function of drainage area (A)

$$h = \alpha A^{\beta} \quad (3)$$

where α and β are empirical values representing local physiography (geology, topography, and climate), basin hydrology, and sediment supply. Bankfull depths were determined from 5-10 cross-sectional surveys in each of the 121 stream reaches. Results demonstrate a slight dependence on regional geology (granitic versus volcanic lithologies) (Figure 11). Similar to channel slope, there can be a two-fold error in prediction of bankfull depth from these data (Figure 12).

Assuming that the critical Shields stress can be approximated by the bankfull value ($\tau^*_c \approx \tau^*_{bf} = \tau/[(\rho_s-\rho)gD_{50}]$) (Buffington and Montgomery 1999; Buffington et al. 2004), τ^*_{bf} was predicted as a function of bankfull shear stress (τ) using observed field values (Figure 13)

$$\tau^*_c \approx \tau^*_{bf} = k\tau^n = k(\rho g h S)^n \tag{4}$$

where k and n are empirical values that vary with channel type and local watershed conditions (Buffington et al. 2004).

Finally, the above relationships for h and τ^*_{bf} were inserted into equation (2), yielding

$$D_{50} = \frac{(\rho \alpha A^{\beta} S)^{1-n}}{(\rho_s - \rho) k g^n} \tag{5}$$

Equation (5) indicates that reach-average median grain size (D_{50}) can be predicted as a function of drainage area (A) and slope (S), values that are readily determined from a digital elevation model. Reach-average values of D_{50} predicted from (5) are then compared to preferred spawning-gravel sizes to determine the availability and spatial distribution of suitable spawning habitat in the basin. Preferred spawning gravel sizes for Chinook salmon were determined from field observations of redd density versus reach-average grain size (Figure 14). Although redds occurred in reaches with a wide range of median particle sizes, the highest redd densities occurred over a relatively narrow range of D_{50} values between 16 and 51 mm, which we defined as the suitable spawning range. These data also show a preference for pool-riffle channel types (morphologic definitions of Montgomery and Buffington (1997; 1998)).

Results & Conclusions

Figure 15 shows predicted values of reach-average median grain size across the basin, with reaches categorized as either suitable (D_{50}=16-51 mm) or unsuitable (D_{50}<16, or >51 mm) for Chinook salmon spawning. Predicted spawning reaches were compared to observed redd locations, using an eight year record (1995-2002) of aerial surveys that has identified 5,135 redds (Thurow 2000 and ongoing). Results demonstrate good agreement between predicted and observed spawning sites (Figure 16), with 68% of the stream network predicted to be suitable for spawning and 87% of redds located in these areas (Table 4). Thirteen percent of the redds occurred in reaches that we predicted to be too coarse for spawning (Table 4), but redd densities were roughly three times smaller in those reaches than in reaches predicted to be suitable (Figure 17).

Results also demonstrate that Chinook redds are not evenly distributed throughout the predicted suitable habitat, but tend to be clustered at the upper ends of the historic stream network (Figure 16). Potential causes for the observed clustering include: depressed population sizes and preferential selection of the best spawning sites; loss of Chinook salmon phenotypes that once spawned in currently underutilized habitats, and fidelity of remaining subpopulations; and constraints imposed by environmental factors other than substrate size (e.g., stream temperature, velocity, scour regime, winter icing, hyporheic flow, etc.). We also note that the highest redd densities tend to occur in broad alluvial valleys (Figure 18). Channels in these areas are typically

low-gradient pool-riffle reaches that commonly contain suitable spawning substrates, however D_{50} sizes tend to be on the low end of what is considered suitable for Chinook salmon (typically 10-20 mm) (see Kondolf and Wolman (1993) for a review of preferred substrate sizes). Marginal substrate size may be offset by favorable hyporheic flow through these alluvial valleys (e.g., Baxter and Hauer, 2000; Tonina 2005). Alternatively, the extensive side-channel habitat typical of these valleys may increase offspring success, resulting in relatively larger densities of returning fish.

Comparisons between predicted and observed reach-average D_{50} values indicate up to a three-fold error in predictions (Figure 19), largely driven by errors in predicting channel slope (Figure 10) and flow depth (Figure 11), which cascade through the grain-size predictions (Equations (2-5)). Future work will seek to minimize these errors and to explore factors other than grain size that may influence spawning site selection.

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Table 1. *A priori* candidate models composed of factors that potentially affect occupancy of suitable patches for Chinook salmon in the upper Middle Fork Salmon River.

Model	Model type	Candidate models[a]
1	Global	Size, connectivity, quality (PC1-PC4)
2	Geometry	Connectivity, size
3	Quality	PC1, PC2, PC3, PC4
4	Quality	PC1, PC2
5	Quality	PC1, PC3
6	Quality	PC1, PC4
7	Hybrid	Connectivity, size, PC1, PC2
8	Hybrid	Connectivity, size, PC1, PC3
9	Hybrid	Connectivity, size, PC1, PC4
10	Hybrid	Connectivity, size, PC1
11	Hybrid	Connectivity, PC1
12	Hybrid	Size, PC1

[a]All models contain a categorical stream effect.

Table 2. Model selection results for logistic regression analysis of factors that affected Chinook salmon occupancy of suitable patches from 1995-2004. Models are ranked from most plausible ($\Delta AIC_c = 0$) to least plausible; p is the number of parameters. The ratio of Akaike weights (w_I/w_i) indicates the plausibility of the best-fitting model compared to other models.

Candidate model[a]	Log likelihood	p	ΔAIC_c[b]	Akaike weight (w_i)	w_I/w_i
2. Connectivity, size	-158.8	4	0.00	0.41	1.00
10. Connectivity, size, PC1	-157.9	5	0.82	0.27	1.51
9. Connectivity, size, PC1, PC4	-156.9	6	1.91	0.16	2.60
8. Connectivity, size, PC1, PC3	-157.4	6	2.89	0.10	4.25
7. Connectivity, size, PC1, PC2	-157.8	6	3.74	0.06	6.49
1. Connectivity, size, PC1, PC2, PC3, PC4[c]	-156.5	8	7.72	0.01	47.5
11. Connectivity, PC1	-170.2	4	22.8	0.00	8.9×10^4
12. Size, PC1	-253.7	4	190	0.00	1.5×10^{41}
5. PC1, PC3	-258.4	4	199	0.00	1.8×10^{43}
3. PC1, PC2, PC3, PC4	-257.6	6	203	0.00	1.4×10^{44}
4. PC1, PC2	-260.6	4	204	0.00	1.6×10^{44}
6. PC1, PC4	-261.4	4	205	0.00	3.5×10^{44}

[a]All models contain a categorical stream effect.
[b]Minimum $AIC_c = 329.04$.
[c]Global model.

Table 3. Parameter estimates and adjusted odds ratios for the three best models predicting probability of patch occupancy by Chinook salmon from 1995-2004. Odds ratios for categorical variables indicate the odds of occupancy for one category level relative to another. Odds ratios for continuous variables indicate the odds of occupancy for every 1-unit change in the variable. Confidence intervals that do not contain 1 are considered statistically significant at $\alpha = 0.05$.

				Adjusted odds ratio		
Model	Parameter	Parameter estimate (SE)	Standardized parameter estimate	Contrast	Estimate	Confidence interval
2	Intercept	-1.7618 (0.2840)				
	Stream 1	-0.1965 (0.2065)		Bear Valley vs. Sulphur	0.345	0.151-0.788
	Stream 2	-0.6702 (0.1984)		Marsh vs. Sulphur	0.215	0.096-0.479
	Size	0.4074 (0.0937)	0.74		1.503	1.251-1.806
	Connectivity	0.0452 (0.0053)	2.10		1.046	1.035-1.057
10	Intercept	-1.6574 (0.2921)				
	Stream 1	-0.4175 (0.2626)		Bear Valley vs. Sulphur	0.244	0.092-0.644
	Stream 2	-0.5763 (0.2089)		Marsh vs. Sulphur	0.208	0.093-0.466
	Size	0.3816 (0.0947)	0.69		1.465	1.217-1.763
	Connectivity	0.0453 (0.0053)	2.10		1.046	1.035-1.057
	PC1	-0.1260 (0.0911)	-0.15		0.882	0.737-1.054
9	Intercept	-1.6906 (0.2967)				
	Stream 1	-0.4324 (0.2630)		Bear Valley vs. Sulphur	0.242	0.091-0.640
	Stream 2	-0.5553 (0.2097)		Marsh vs. Sulphur	0.214	0.095-0.481
	Size	0.3856 (0.0955)	0.70		1.471	1.219-1.773
	Connectivity	0.0459 (0.0054)	2.13		1.047	1.036-1.058
	PC1	-0.1362 (0.0924)	-0.16		0.873	0.728-1.046
	PC4	0.1566 (0.1148)	0.11		1.170	0.934-1.465

Table 4. Comparison between reach-scale substrate classification and distribution of Chinook salmon redds in the MFSR.

Substrate size category (mm)	% of stream network	% of redds (n = 5135)
< 16	0%	0%
16 – 51 (suitable)	67.8%	87.3%
>51	32.2%	12.7%

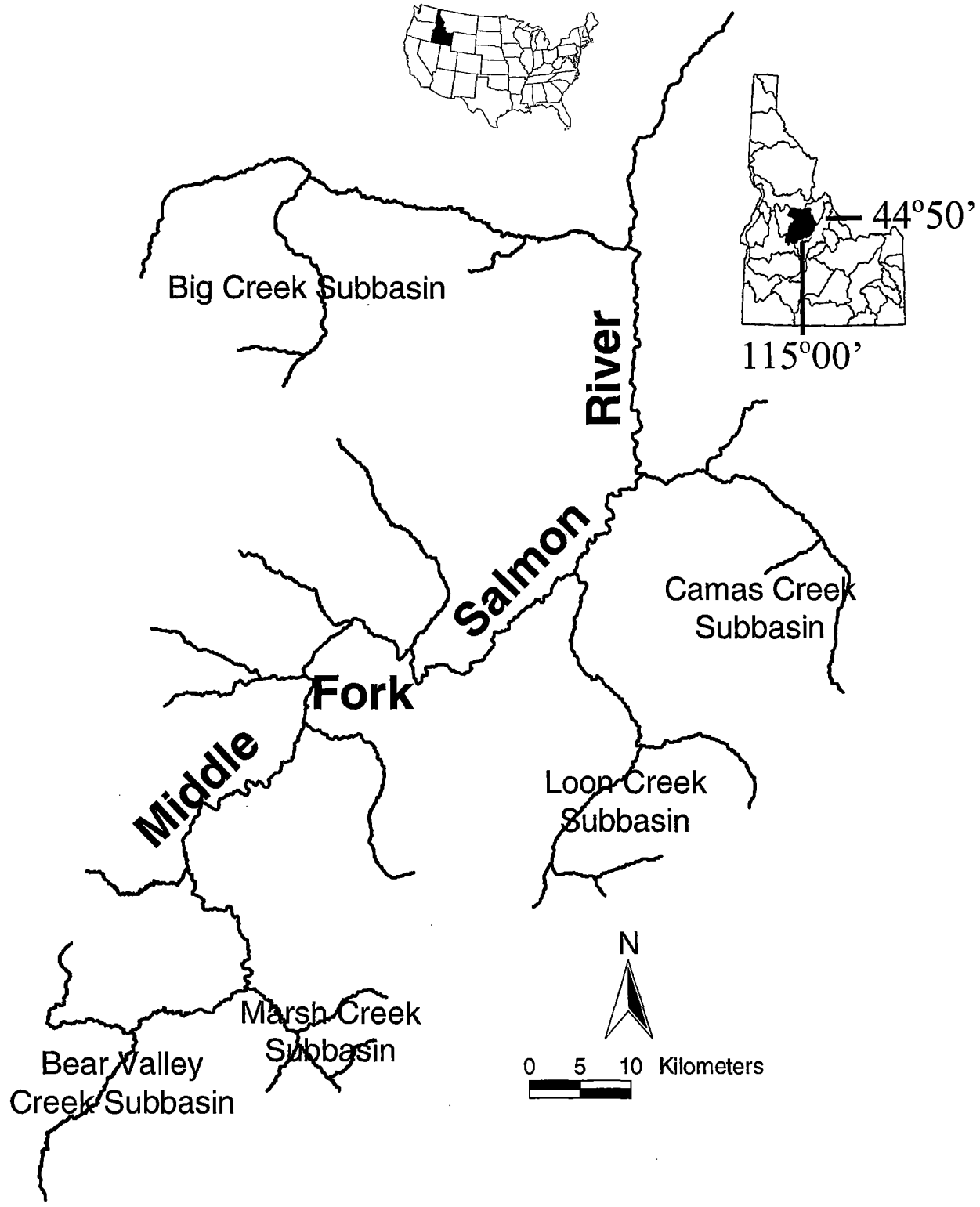

Figure. 1. Stream network in the Middle Fork Salmon River that was accessible to Chinook salmon and was sampled during aerial surveys for redds from 1995-2005.

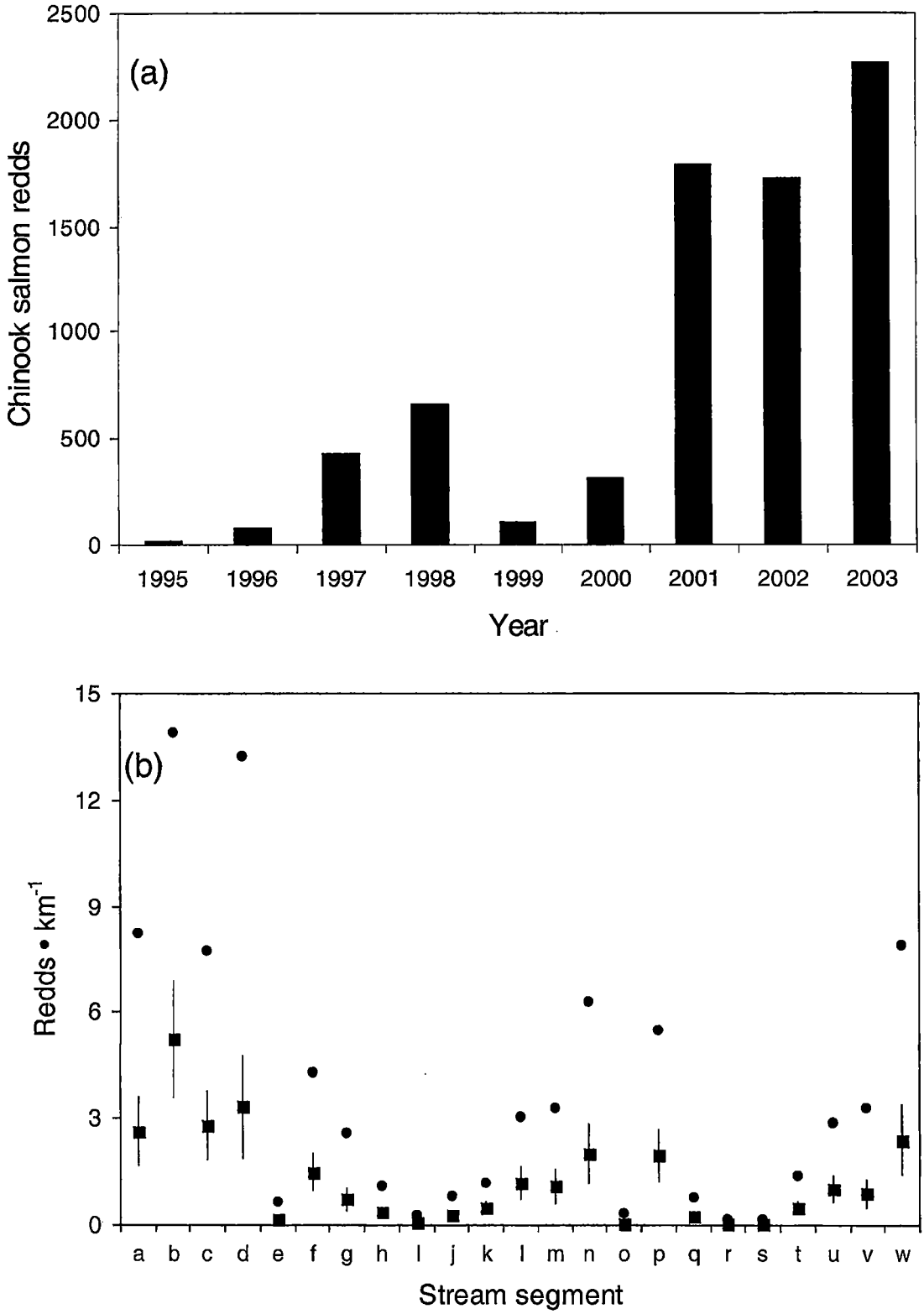

Figure. 2. Basinwide totals for Chinook salmon redds *(Oncorhynchus tshawytscha)* counted during aerial surveys from 1995-2003 (panel a). Mean redd densities (± 1 standard error) within stream segments (panel b). Points above mean values indicate the maximum number of redds that occurred within a stream segment during this study.

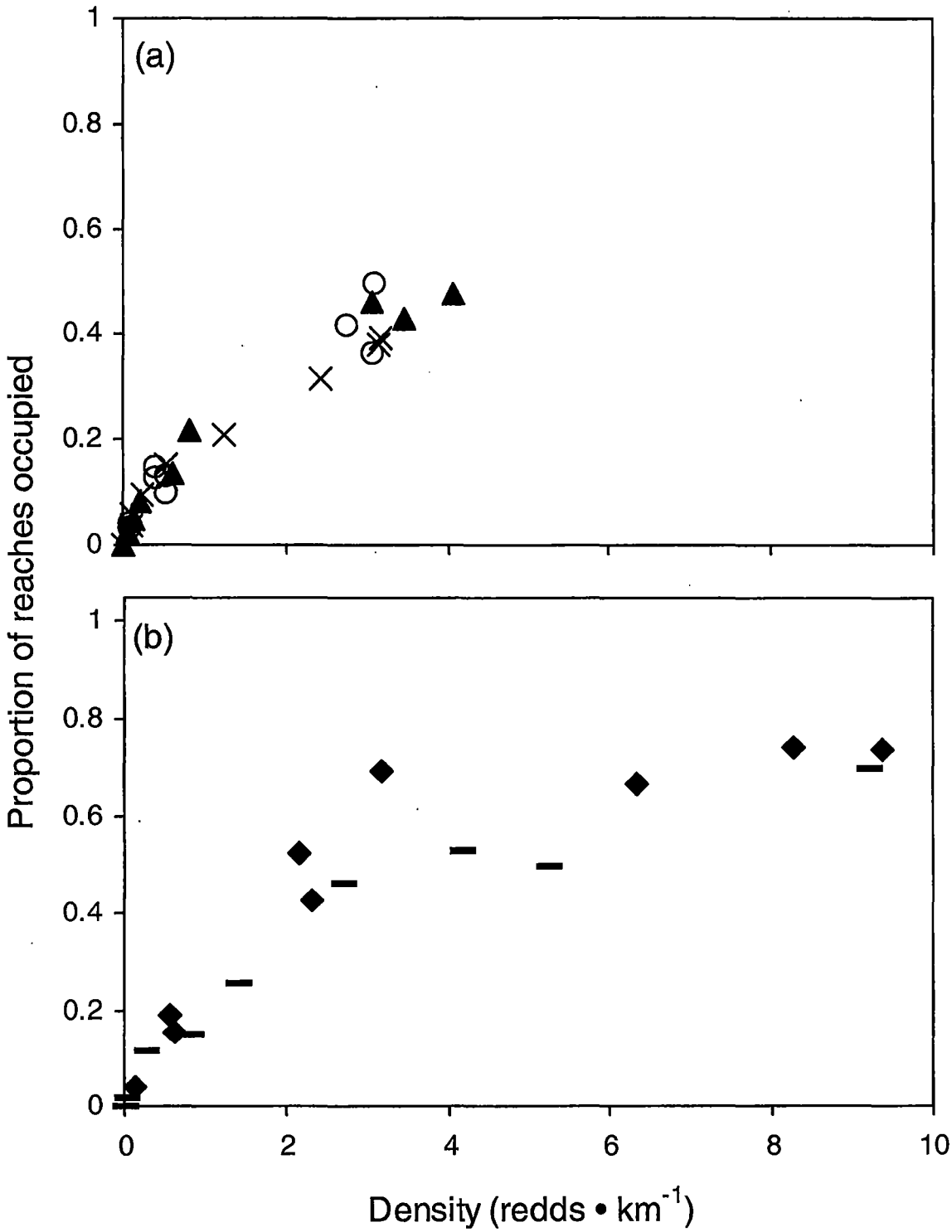

Figure 3. Occurrence of Chinook salmon redds within five subbasins in the Middle Fork Salmon River. Panel (a) depicts patterns in subbasins where population expansion was ongoing (▲= Loon Creek, X = Camas Creek, O = Big Creek); panel (b) depicts patterns in subbasins where population expansion appears to have reached an upper limit (♦ = Bear Valley Creek, — = Marsh Creek).

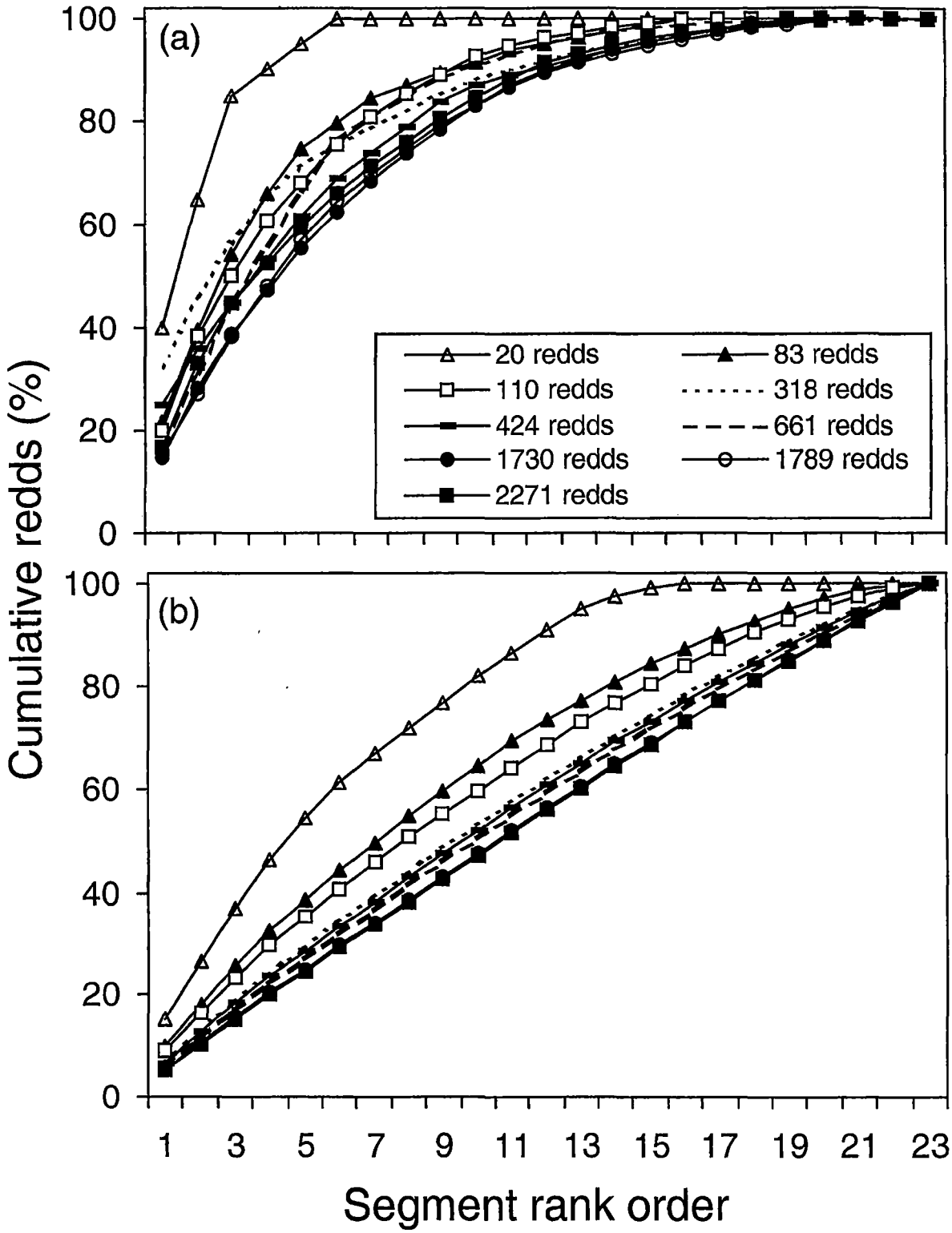

Figure 4. Rank-ordered cumulative distribution curves for observed redd locations (panel a) and randomized redd locations (panel b).

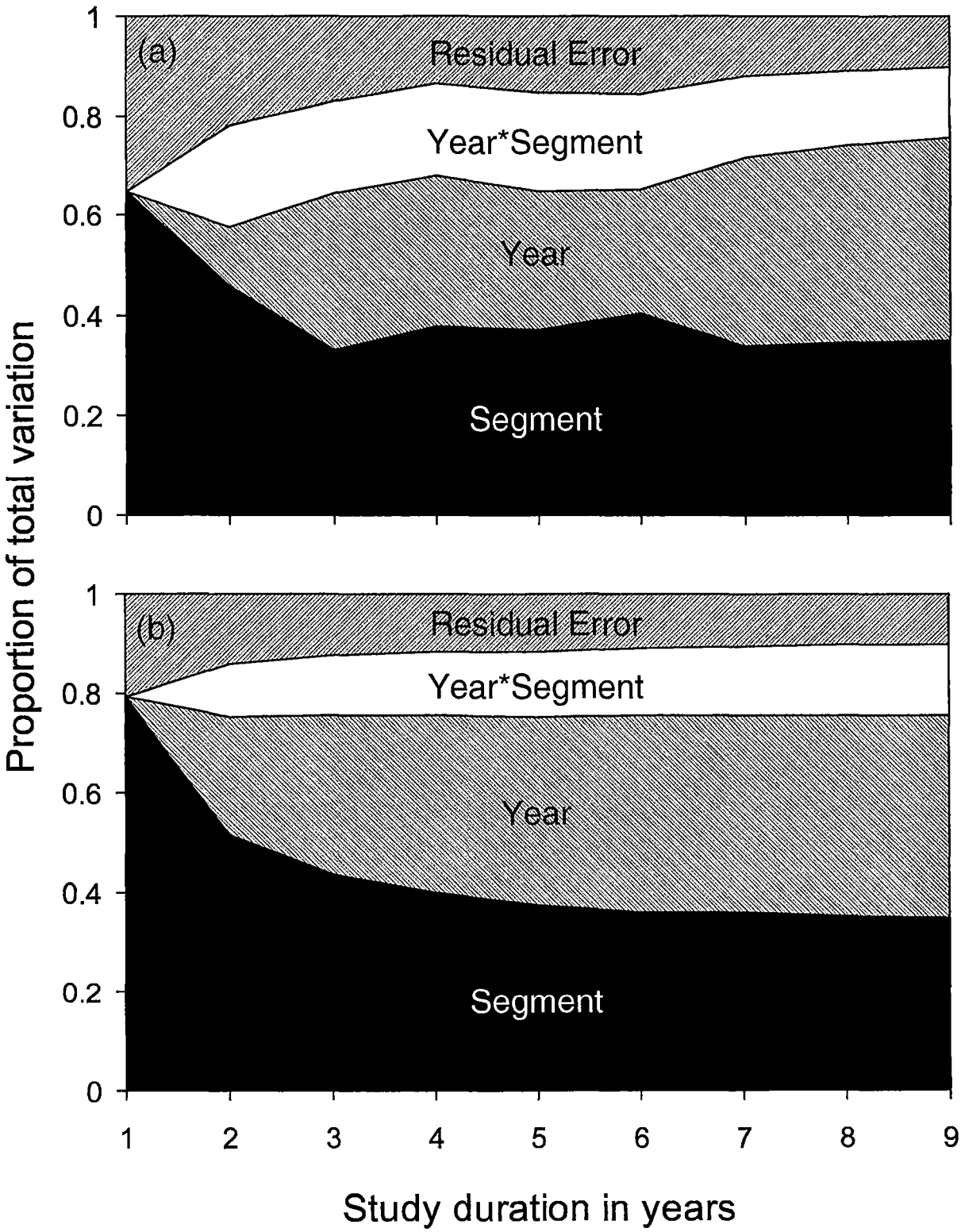

Figure 5. Relative importance of variance components as a function of study duration. Panel (a) depicts the pattern derived from the observed data sequence; whereas panel (b) depicts the average pattern derived from different yearly combinations of data.

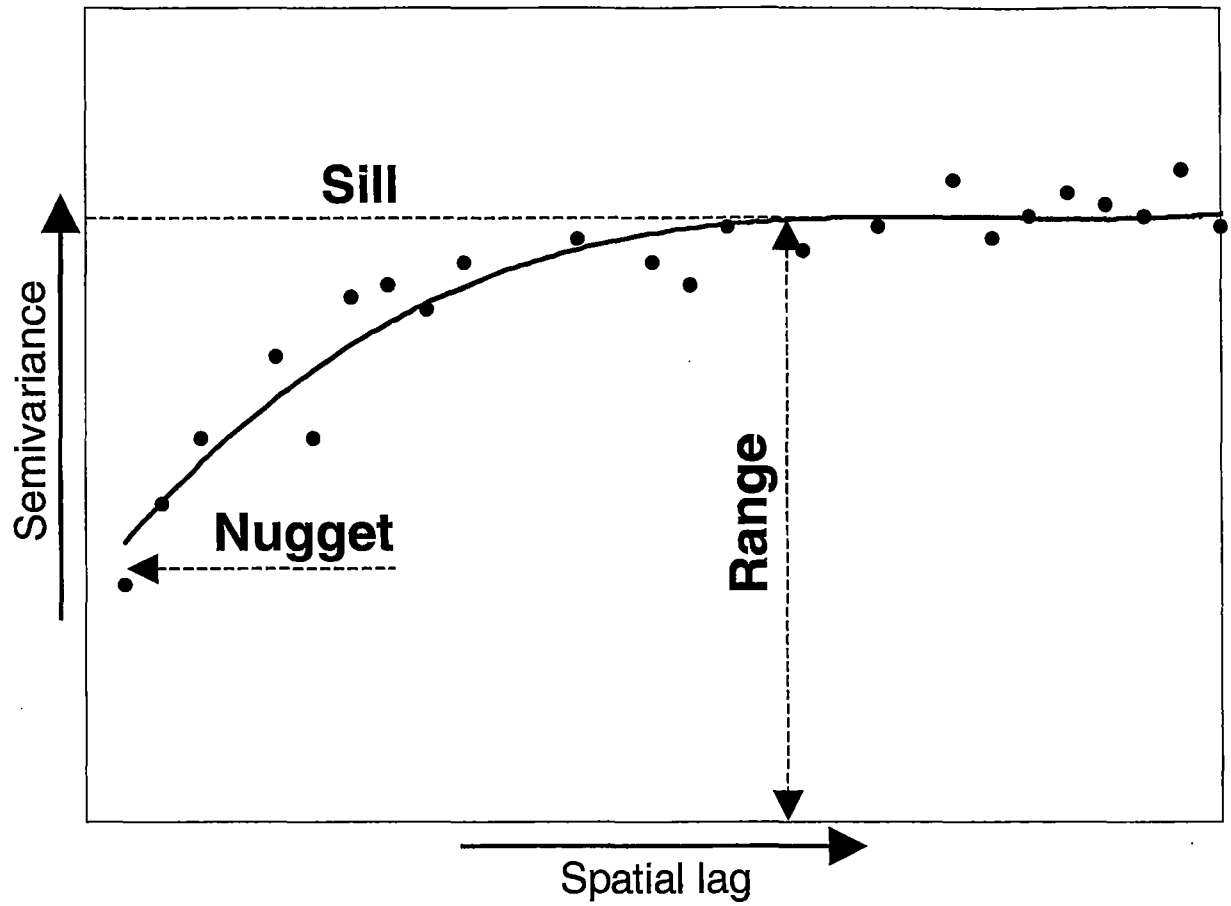

Figure 6. Components of the semivariogram. A nonzero Y-intercept is referred to as a nugget and indicates variation at distances less than the sampling lag. The sill is the semivariance asymptote, which provides a measure of the total sampling variation. The range is the spatial lag distance at which the semivariance reaches an asymptote and indicates where spatial dependence ends.

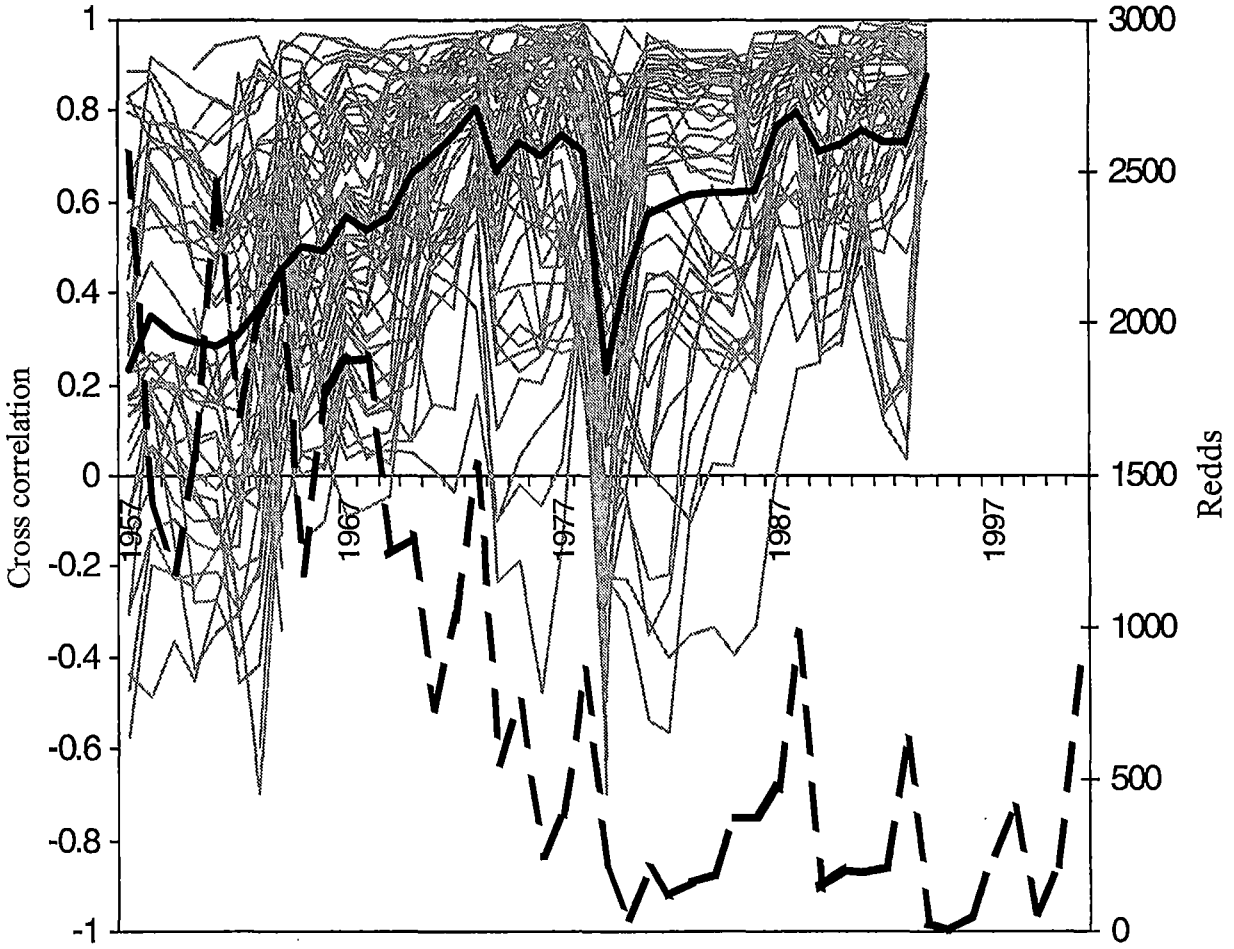

Figure 7. Temporal trends in cross correlations among all pairwise combinations of redd counts at IDFG transects. Solid dark line represents the mean cross correlation; dashed line represents the total Chinook salmon redd count from IDFG trend sites in the MFSR.

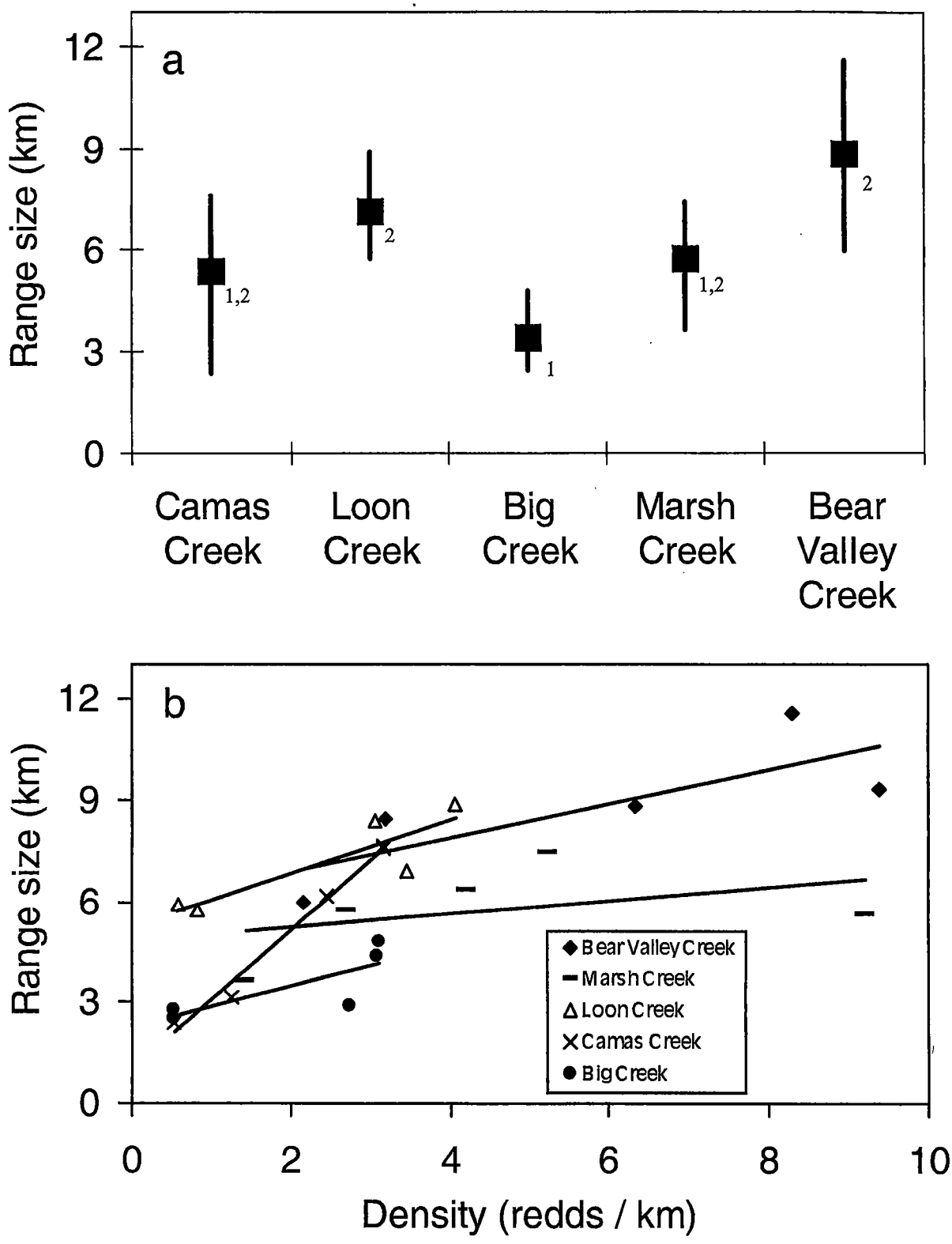

Figure 8. Mean range sizes for five subbasins (panel a). Error bars denote the range of observed values; subscripts denote statistical differences. Slopes of relationships between range size and redd density for five subbasins in the Middle Fork Salmon River (panel b).

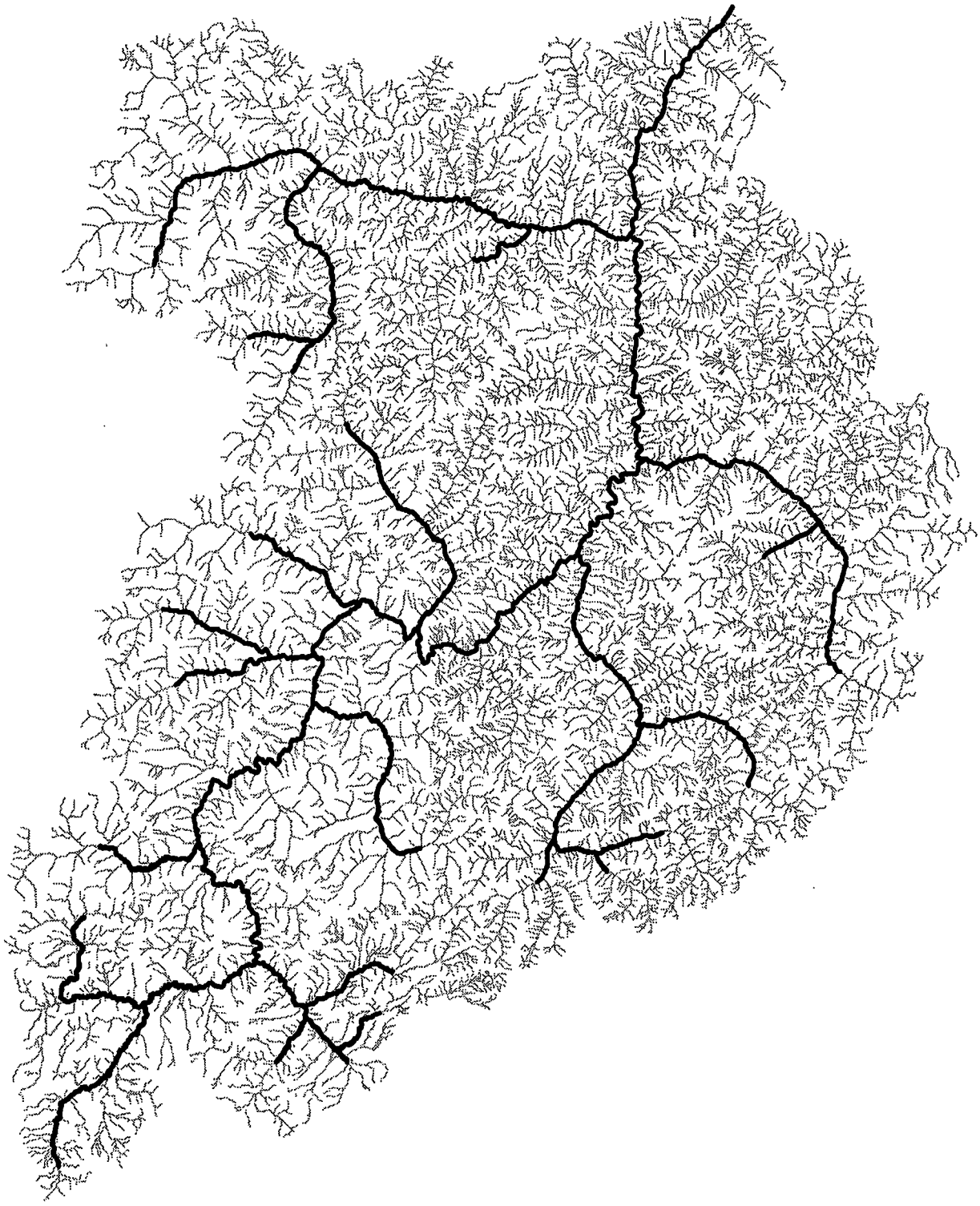

Figure 13. Reduced stream network (heavy black line) used in the current analysis.

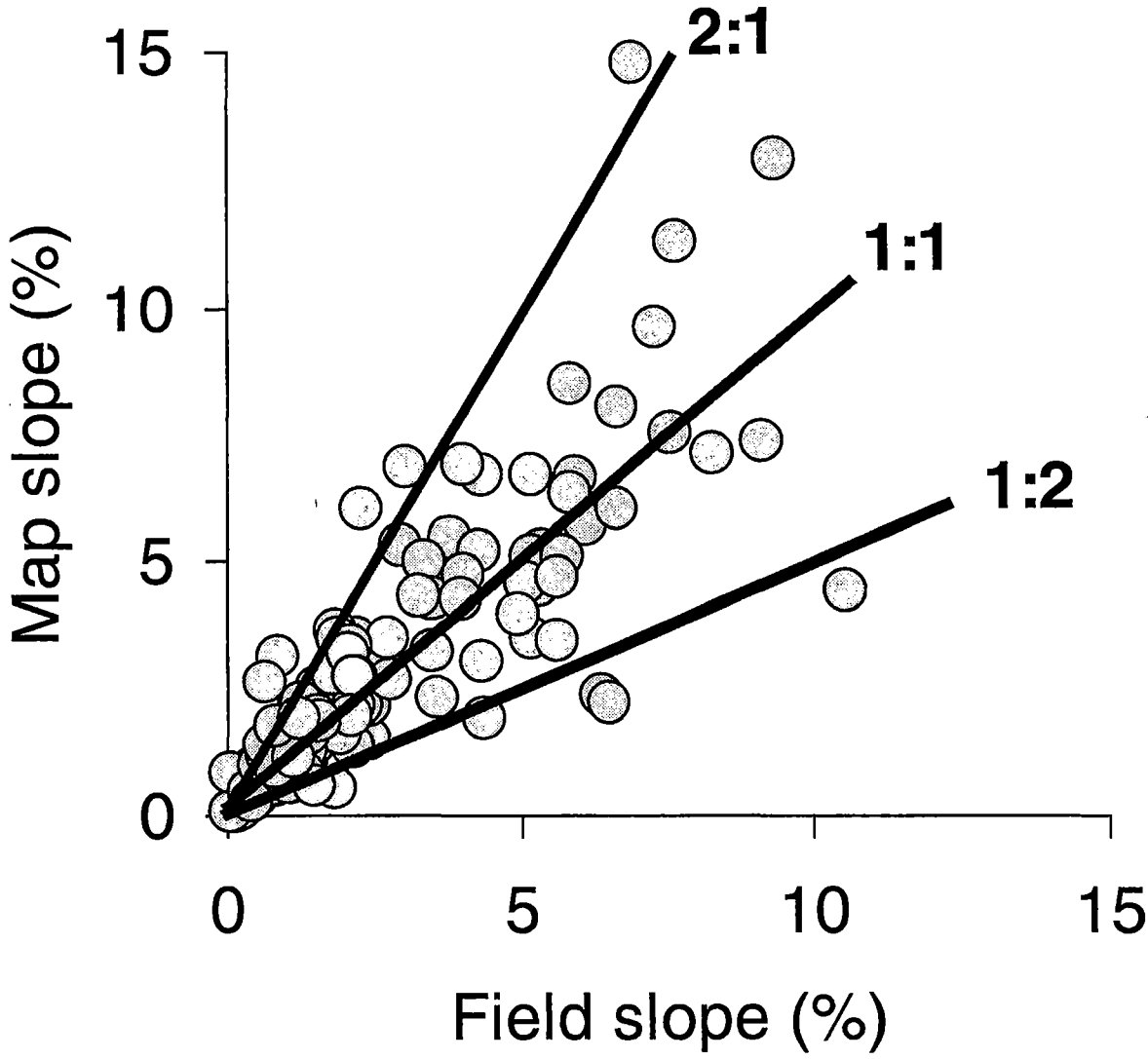

Figure 10. Comparison of map versus field slopes for study sites in the Middle Fork Salmon River basin.

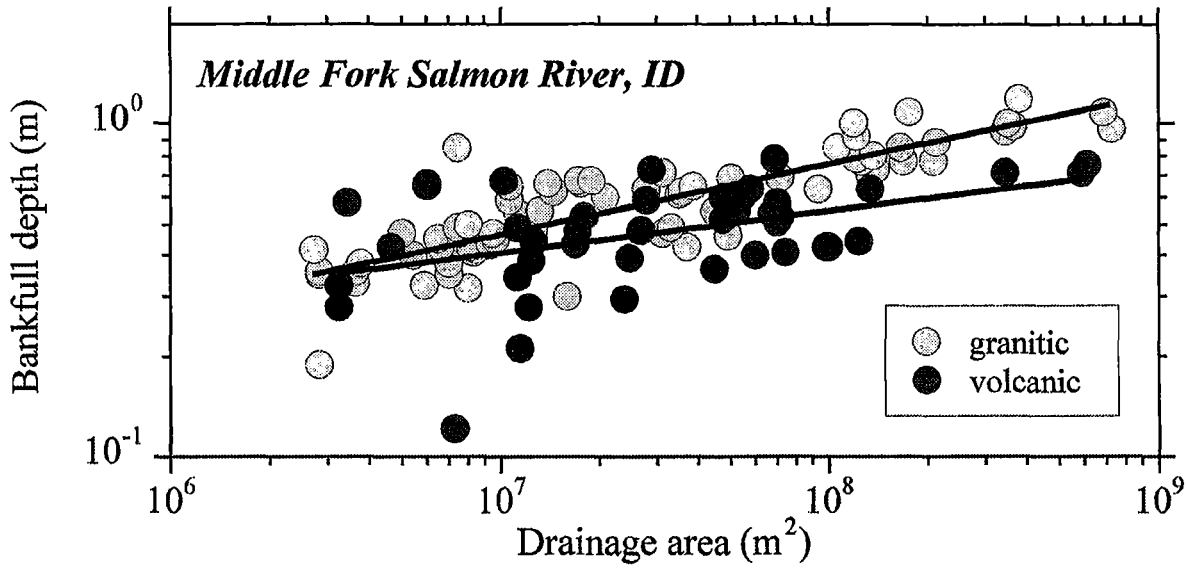

Figure 11. Bankfull depth as a function of drainage area, stratified by local geology.

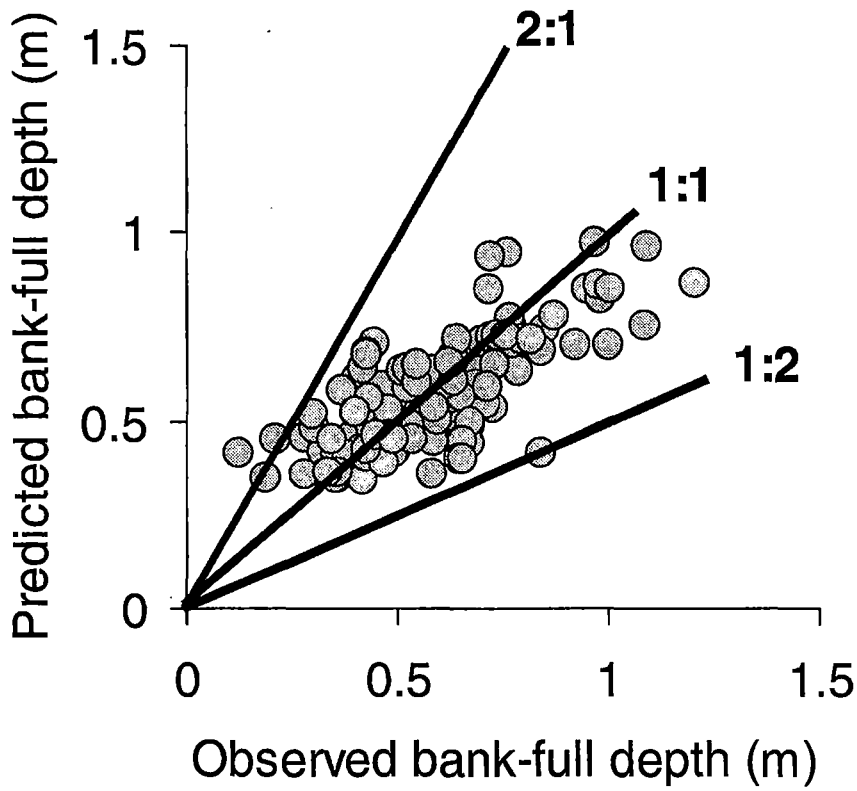

Figure 12. Predicted versus observed bankfull depths for study sites in the Middle Fork Salmon River basin.

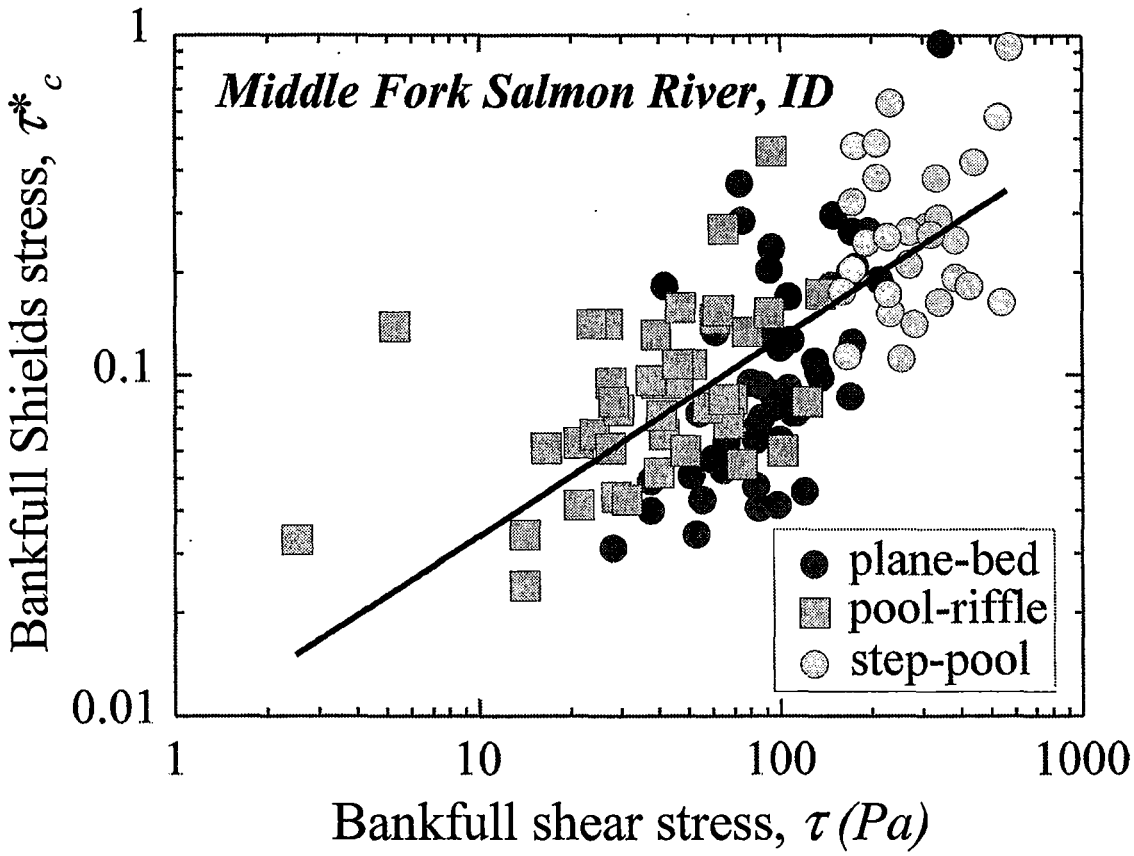

Figure 13. Bankfull Shields stress as a function of total boundary shear stress, stratified by Montgomery and Buffington's (1997; 1998) channel reach types.

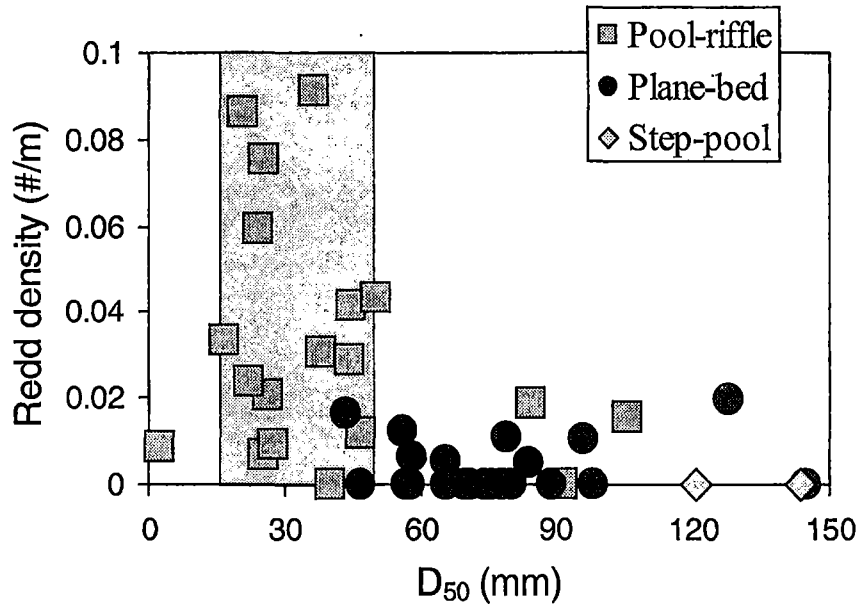

Figure 14. Chinook salmon redd densities versus reach-average median grain size (D_{50}) for channels in the Middle Fork Salmon River (channel type definitions of Montgomery and Buffington (1997; 1998)). Shaded box indicates the highest redd densities and our consequent definition of preferred D_{50} sizes for spawning (16-51 mm).

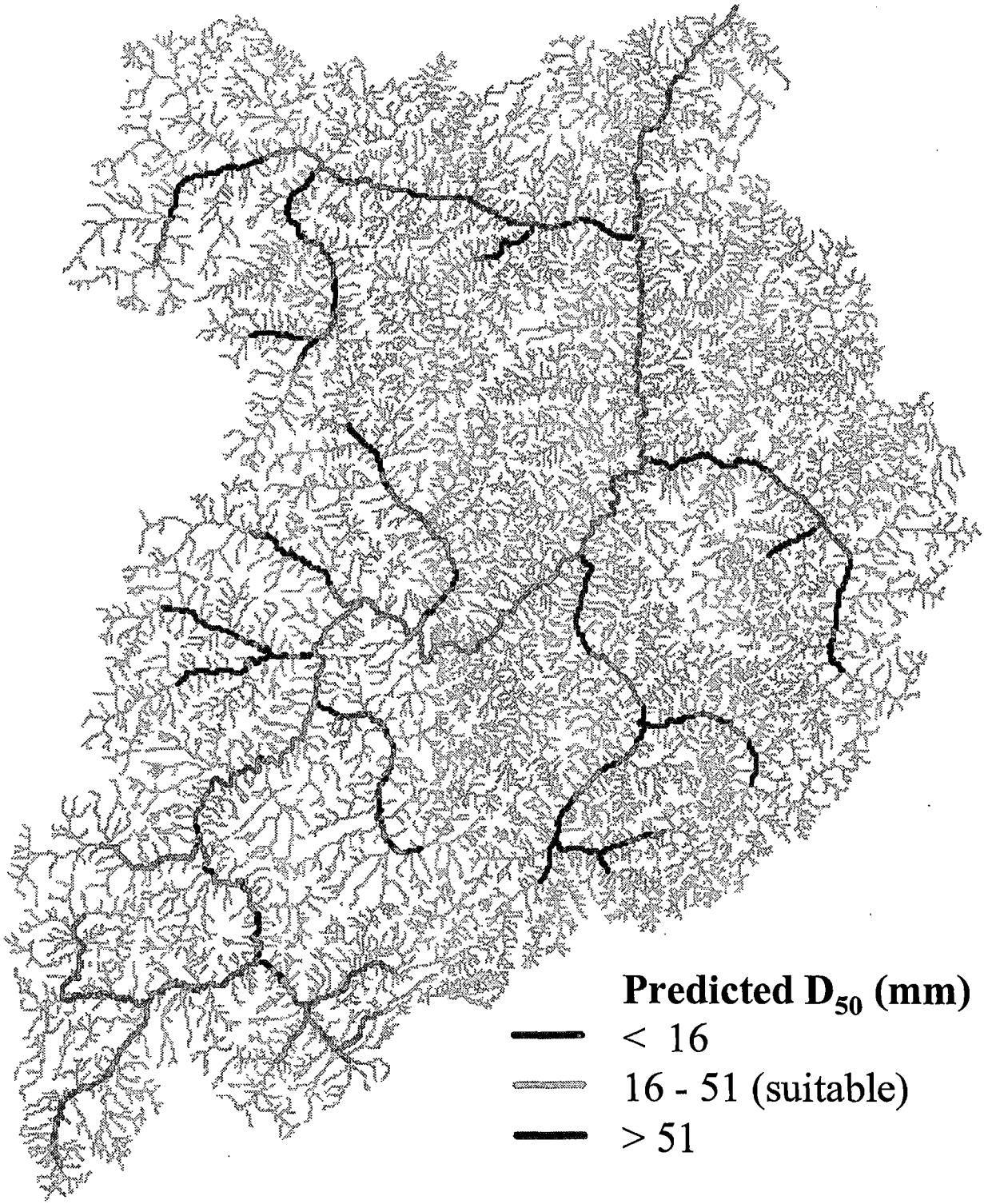

Figure 15. Predicted locations of channel reaches containing Chinook salmon spawning gravels in the Middle Fork Salmon River. Predictions were made within a reduced channel network, representing the observed historic range of Chinook salmon spawning (colored segments).

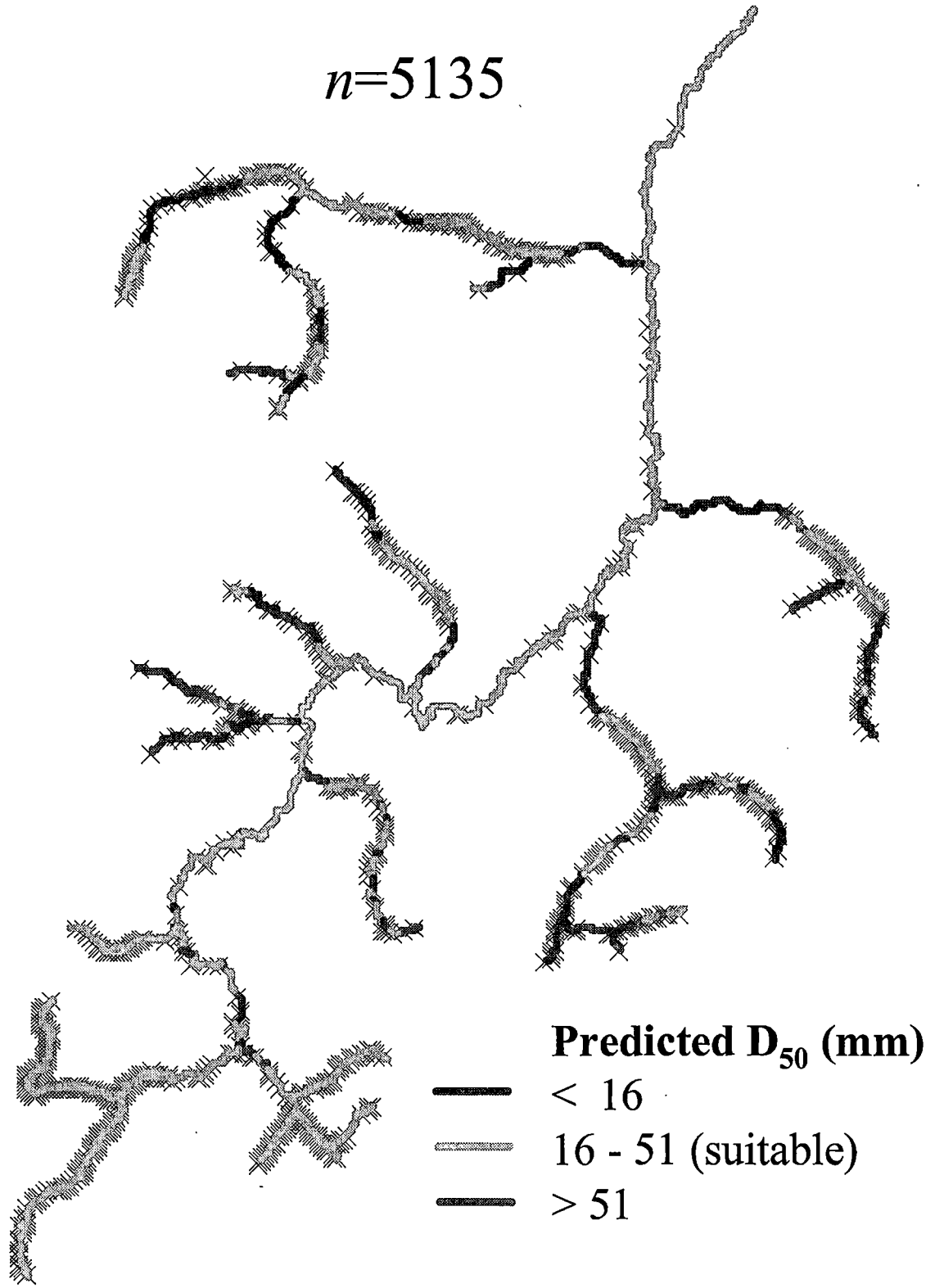

Figure 16. Predicted spawning gravel availability versus observed Chinook salmon redds (x's) in the Middle Fork Salmon River (1995-2002).

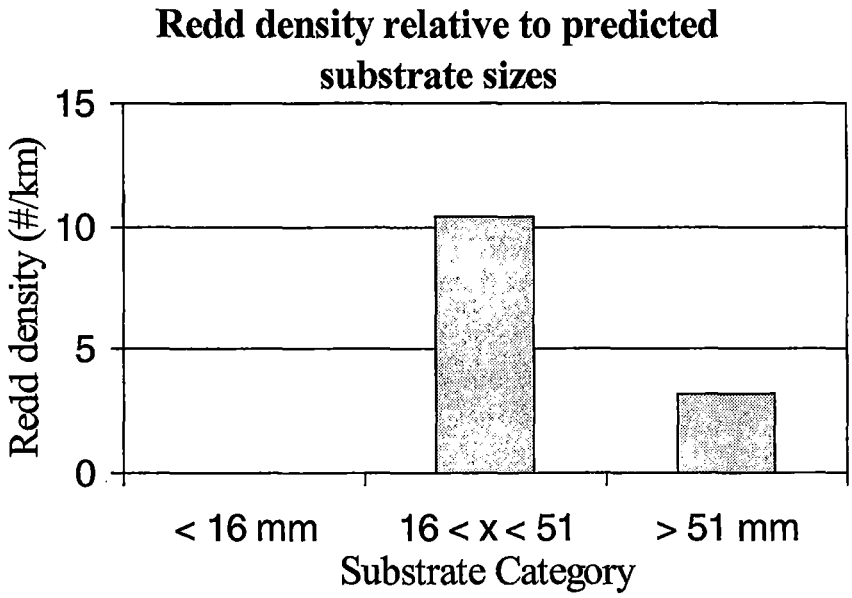

Figure 17. Chinook salmon redd densities within the predicted reach types.

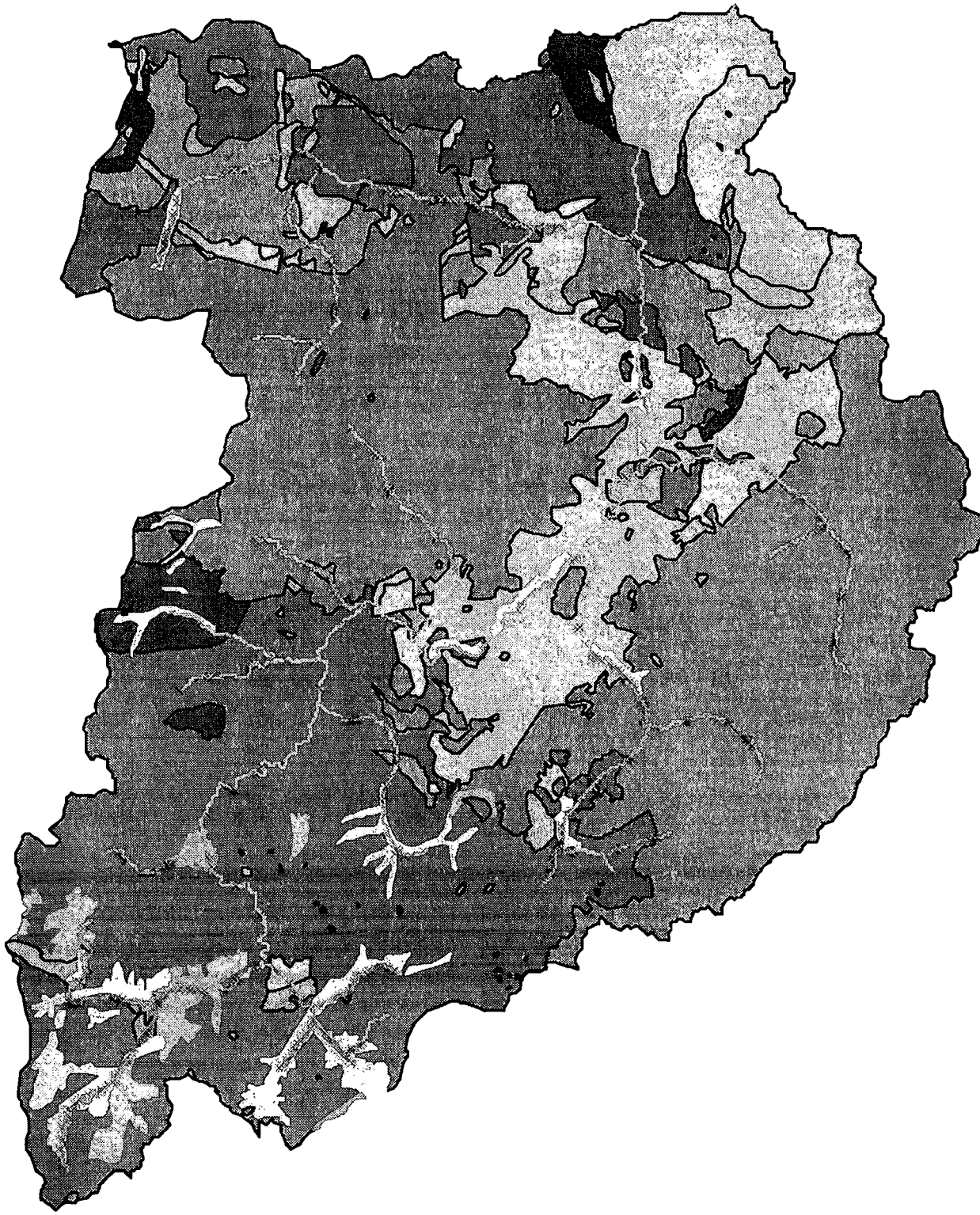

Figure 18. Channel network (cyan segments) and locations of Chinook salmon redds (x's) overlain on basin geology of the Middle Fork Salmon River. Yellow and green units are alluvium.

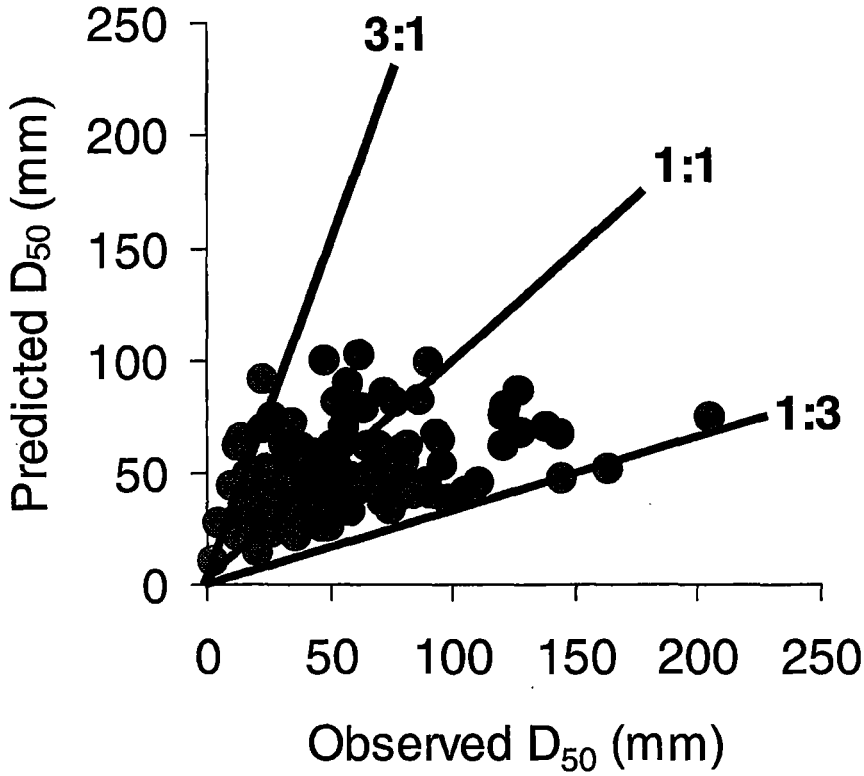

Figure 19. Predicted versus observed reach-average median grain size (D_{50}) in the Middle Form Salmon River.

APPENDIX A

Peer-Reviewed Manuscripts

Buffington, J.M., Isaak, D.J., Thurow, R.F., and D. Nagel. In prep. Geomorphic controls on basin-scale availability of Chinook salmon spawning habitat in the Middle Fork Salmon River. Canadian Journal of Fisheries and Aquatic Sciences.

Isaak, D.J., and R.F. Thurow. 2006. Network-scale patterns of spatial and temporal variation in Chinook salmon redd distributions: patterns inferred from spatially continuous replicate surveys. Canadian Journal of Fisheries and Aquatic Sciences 63:000-000.

Isaak, D.J., and R.F. Thurow. Submitted. Relative effects of density and habitat heterogeneity on scale of spatial synchrony in Chinook salmon breeding distributions. Ecography.

Isaak, D.J., R.F. Thurow, B.E. Rieman, and J.B. Dunham. Submitted. Relative roles of habitat size, connectivity, and quality on occupancy of spawning patches by Chinook salmon. Transactions of the American Fisheries Society.

Isaak, D.J., R.F. Thurow, B.E. Rieman, and J.B. Dunham. 2003. Temporal variation in synchrony among Chinook salmon redd counts from a wilderness area in central Idaho. Canadian Journal of Fisheries and Aquatic Sciences 60:840-848.

Posters

Isaak, D.J., R.F. Thurow, B.E. Rieman, and J.B. Dunham. 2005. Conservation implications of spatial and temporal synchrony among Chinook salmon populations. American Fisheries Society annual meeting, Anchorage, AK.

Thurow, R.F., and D.J. Isaak. 2005. A spatially continuous, temporally dimensioned redd count database for examining network-scale dynamics of Chinook salmon. American Fisheries Society annual meeting, Anchorage, AK.

Buffington, J.M., D.J. Isaak, and R.T. Thurow. 2002. Geomorphic controls on watershed-scale availability of Chinook salmon spawning habitat in the Middle Fork Salmon River. Western Division American Fisheries Society Meeting, Spokane, WA.

Oral Presentations

Buffington, J.M., D.R. Montgomery, H.M. Greenberg, D.J. Isaak, and R.T. Thurow. (invited) 2005. Basin-scale availability of salmonid spawning gravel as influenced by channel type and hydraulic roughness in mountain catchments. Seminar Series. Department of Biological Sciences, Idaho State University. Pocatello, ID, April 21, 2005.

Isaak, D.J., Thurow, R.F., Rieman, B.E., and Dunham, J.B. 2005. Roles of habitat size, connectivity, and quality on patch occupancy by Chinook salmon: implications for restoration. American Fisheries Society annual meeting, Anchorage, AK.

Isaak, D.J., Thurow, R.F., Rieman, B.E., Neville, H.M. 2005. Assessing the Relative Roles of Environmental Factors on Population Scaling: An Example with Chinook Salmon. Eos Transactions of the American Geophysical Union, 86(18), Joint Assembly Supplement, Abstract B42A-02, New Orleans, LA.

Thurow, R.F., D.J, Isaak, and J.M. Buffington. (invited) 2005. Investigating biophysical processes within a large wilderness river basin to advance understanding of the factors influencing persistence of Chinook salmon. 8th World Wilderness Congress, Anchorage, AK.

Buffington, J.M., D.J. Isaak, and R.F. Thurow. (invited) 2004. Geomorphic controls on the distribution of salmonid spawning habitat in mountain basins. The Biobío River Scientific Forum. University of Concepción, Chile, March 29, 2004.

Thurow, R.F. and D.J. Isaak. 2004. Utility of spatially continuous, basinwide redd counts for examining spatial and temporal dynamics of Chinook salmon. National American Fisheries Society Annual Meeting, Madison, WI.

Isaak, D.J., and R.T. Thurow. 2004. How much is enough? Using semivariograms and spatiotemporally dimensioned census data to understand the geography of Chinook salmon populations. North American Benthological Society and Western Division American Fisheries Society meetings.

Buffington, J.M., D.J. Isaak, and R.F. Thurow. (invited) 2003. Hydraulic control on the spatial distribution of Chinook salmon spawning gravels in central Idaho: integrating reach-scale predictions via digital elevation models. Eos Transactions of the American Geophysical Union, 84(46), Fall Meeting Supplement, Abstract H32F-01, San Francisco, CA.

Buffington, J.M., D.J. Isaak, and R.F. Thurow. (invited) 2003. Assessing the availability of salmonid spawning gravels at watershed, reach and subreach scales: effects of channel type & hydraulic roughness on streambed texture. Symposium on physical factors affecting salmon spawning and egg survival to emergence: integrating science and remediation management, National American Fisheries Society Meeting, Quebec City, Quebec.

Isaak, D.J., R.F. Thurow, and J.M. Buffington. (invited) 2003. Physical features influencing salmonid spawning distributions at multiple geographic scales: insights from chinook salmon in a wilderness basin. Symposium on physical factors affecting salmon spawning and egg survival to emergence: integrating science and remediation management, National American Fisheries Society Meeting, Quebec City, Quebec.

Isaak, D.J., R.F. Thurow, B.E. Rieman, and J.B. Dunham. 2003. Long-term temporal variation in synchrony among Chinook salmon redd counts from a wilderness area in central Idaho. Colorado/Wyoming chapter of the American Fisheries Society annual meeting and the Idaho chapter of the American Fisheries Society annual meeting.

Thurow, R.F. and D.J. Isaak. 2003. Temporal and spatial dynamics of Chinook salmon in the Middle Fork Salmon River, Idaho. Idaho Chapter of the American Fisheries Society annual meeting, Boise, ID.

Isaak, D.J., and R.T. Thurow. 2002. Patterns in spatial synchrony among Chinook salmon redd counts within the Middle Fork Salmon River: implications for metapopulation dynamics. Western Division American Fisheries Society Meeting, Spokane, WA.